ANATOMIC STUDIES ON
PROBOSCIDEA PARVIFLORA AND PROBOSCIDEA LOUISIANICA

by

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Major Professor

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INTRODUCTION

The genus Proboscidea, of the family Martyniaceae, contains nine species. These are mostly tropical and subtropical, annual and perennial herbs. The only species found in Kansas, Proboscidea louisianica (Miller) Thell., is a large spreading annual. This species has opposite or alternate leaves (10-30 cm long) that are cordate with entire or sinuate margins. The large flowers, with corollas up to 5 cm long, are white or yellowish and mottled or blotched with reddish purple or occasionally reddish violet. The fruit of this taxon is a capsule with a recurved tip. The pericarp is differentiated into exocarp, mesocarp and endocarp; at maturity the exocarp and fleshy mesocarp are sloughed off, leaving the stony endocarp which dehisces at the distal end resulting in two curved horns. The common names associated with this plant are devil's claw and unicorn plant, the appearance of the fruit being responsible for these terms.

Proboscidea parviflora Wooten & Standley, a species found in Texas westward to Nevada and Utah, is also a large spreading annual which forms a mat up to two meters in diameter. The leaves of this species are broadly triangular to broadly ovate in general outline, nearly entire to very obtusely 5-7 lobed, cordate, and are oppositely to subopposite arranged. The flowers, with corollas 2.5 cm - 3.5 cm long, have dull

yellow throats with a dull purple blotch above, and spreading over the upper lobes. The fruit of P. parviflora is similar to that of P. louisianica, but is slightly more slender.

The purpose of this study was to describe the anatomy of the apparently distinct species P. parviflora and P. louisianica and to compare any salient differences. A problem in seed germination was encountered during attempts to obtain mature plants for the anatomic study, therefore, a study of the effects of different light qualities upon germination has been included. Anderson (in press) has considered some morphological and anatomical aspects of P. louisianica when gibberillic acid was used to break seed dormancy. He observed a retardation in flowering. Along with this retardation, there was an excessive elongation of the hypocotyl which in most cases resulted in the plant falling over; this was therefore considered a poor means of obtaining seedlings, and thus the interest in light quality effect.

REVIEW OF LITERATURE

Taxonomically, the family Martyniaceae was in a state of confusion until Van Eseltine (1929) revised the family. Solereder (1908) included Martynia diandra Glox. (Martynia annua L. according to Van Eseltine) in describing some anatomical features of the Tribe Martynieae in the family Pedaliaceae, which was the scheme of Bentham and Hooker.

Van Eseltine (1929) did a systematic revision of a group he called the Martyniaceae, and established that family as being distinct from the Pedaliaceae, the Bignoniaceae, and the Gesneriaceae into which it had been placed by several authors. Five genera were distinquished in Martyniaceae: Craniolaria, Holoregnia, Proboscidea, Ibicella, and Martynia. According to Van Eseltine's classification, Proboscidea is composed of two subgenera and nine species:

Subgenus: Dissolophia

P. confusa, P. arenaria, P. peruviana,
P. altheaefolia

Subgenus: Eu-proboscidea

P. parviflora, P. sinaloensis, P. triloba,
P. fragrans, P. Jussieui

This systematic treatment had been considered correct until Lawrence (1957) questioned the nomenclatural validity of Van Eseltine's Proboscidea Jussieui. Lawrence (1957) did a nomenclatural review of the species and based his conclusions on the writings of Johann Keller and Philip Miller. According to Lawrence (1957), the generic name, Proboscidea, was introduced by Keller in 1762 when describing the species he called P. Jussieui, but Keller did not follow Linnaean binomial classification throughout his publication. Therefore, the generic name Proboscidea is valid but the epithet Jussieui is invalid. In 1768, Philip Miller described three species under Martynia, one of which was M. louisiana; a correction

was incorporated into this 1768 book which changed the epithet from "louisiana" to "louisianica". This correction was necessary because the name was meant to commemorate the state of Louisiana, not Louis XIV, King of France. The plant Miller described as Martynia louisianica was the same plant Keller described under the name Proboscidea Jussieui, therefore the plant is properly a Proboscidea and Albert Thellung was correct in making the combination Proboscidea louisianica (Miller) Thellung.

Flora Anderson (1922) described the floral development and embryogeny of P. louisianica and P. fragrans. She found that these two species crossed very readily resulting in viable seeds, and that there were no structural differences observed between these species. The endosperm was diploid, resulting from the fusion of the polar nuclei and subsequent mitotic divisions. Anderson's (1922) observations, with respect to P. louisianica, were also reported by Martini (1939).

Anatomically the Martyniaceae have been given little attention. Solereder (1908) mentioned some anatomical features of a species of Martynia, M. annua, but didn't consider any other species in his description of this group of plants. With the exception of Mayberry's (1947) anatomical study of P. louisianica, which he did because of that plant's occurrence in Kansas, this author has found no anatomical data concerning the genus Proboscidea.

METHODS AND MATERIALS

Seed of P. louisianica from Riley Co., Kansas, was supplied by Dr. Loran C. Anderson and seed of P. parviflora from Socorro Co., New Mexico, by Mr. David L. Spellman. These populations are documented in the Kansas State University Herbarium by the voucher specimens, Anderson 2841 and Schaffer 65-01, respectively.

Excised embryos of P. louisianica (each surrounded by a multicellular nucellus) were germinated on moist filter paper in the dark. Each embryo was surrounded by its nucellus because of the mechanical difficulty in removing that tissue. Removal of the nucellus always resulted in considerable damage to the embryo, therefore all embryos used in this study were surrounded by their nucelli. Seedlings were transferred to a garden plot on the Kansas State University campus and grown there during the summer of 1965.

Excised embryos of P. parviflora (each surrounded by a nucellus) were germinated on filter paper moistened with 50ppm gibberillic acid (K-salt of GA_3, Nutritional Biochemicals Corporation, Cleveland, Ohio). When the radicle began to elongate, the seedlings were planted in peat pots in the greenhouse. Once the plants were established (that is the plants did not fall over due to excessive elongation of the hypocotyl, as was the condition in most cases) these plants were transferred to the garden plot beside the P. louisianica plants

and grown during the summer of 1965.

All plant tissue sections were made from living material which had been killed and fixed September, 1965, in Craf V or in formalin-propionic acid-alcohol (Sass, 1963) and stored in the same solutions three days to one year. Materials to be sectioned were first dehydrated in a graded tertiary butyl alcohol series (Johansen, 1940) and embedded in paraffin. These tissues were sectioned at 10-15 microns on a rotary microtome and stained in either a Harris haemotoxylin-safranin-fast green schedule or a tannic acid/ferric chloride-safranin-fast green schedule. Woody materials were soaked in equal parts of glycerin and 70% ethyl alcohol for seven days and then sectioned on a sliding microtome. Wood sections were made at 20 microns and stained with safranin. Macerations of woods were accomplished by the dissociation of the cells in equal parts 10% chromic acid and 10% nitric acid for 4-5 hours at 56°C, followed by dehydration of the tissue through an ethyl alcohol series and staining in safranin. Whole mounts of leaves and floral parts were stained and cleared simultaneously in basic fuchsin in sodium hydroxide (Fuchs, 1963). All sections, macerations, and whole mounts were mounted in Permount.

Equipment used in the germination study included "light boxes" and a Labline growth chamber with banks of cool white fluorescent lamps and white incandescent light bulbs. The "light boxes" were cardboard boxes with portions of the lids

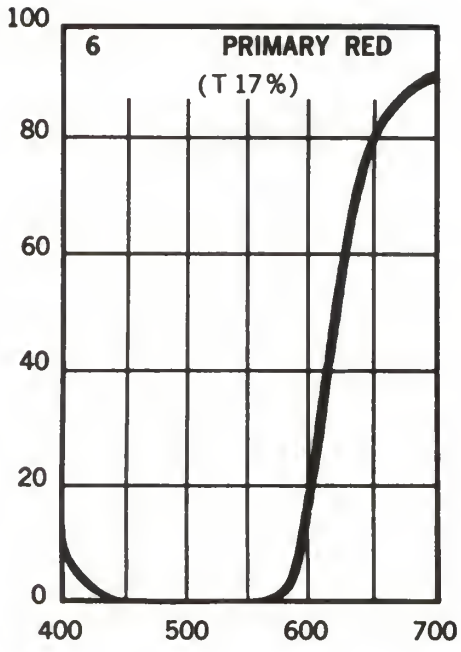
replaced with Cinemoid filters (Klein, 1965) (green, red, blue, and a combination of blue/red to produce far red). See Fig. 1 for the transmittance peaks of these filters. At the level at which the "light boxes" were maintained in the growth chambers the light intensities were 1500 fc to 2000 fc in the 24°C growth chamber and 1100 fc to 1250 fc in the 30°C growth chamber. Excised embryos and intact seeds were placed on moist filter paper in petri dishes which were placed inside the "light boxes". The boxes were then sealed and the entire assemblages were placed in growth chambers maintained at 24°C and at 30°C. There were four replications with 20 excised embryos or intact seeds per replication per light quality.

RESULTS

Germination

There was no germination of fall harvested intact seeds or excised embryos under blue and far red light. The percentage of germination under red and green light were approximately the same. Table I lists germination results of P. louisianica seeds under different light qualities and at the temperatures noted. At 30°C the embryos under red and green light had 50-63 and 78-85 percent germination respectively after 67 hours, whereas there was only 26 percent germination of the embryos under white light after eight days, which was the length of each of these runs.

Fig. 1. The transmittance spectra of the filters used in the germination studies of P. louisianica seeds: a, primary red; b, primary blue; c, primary green.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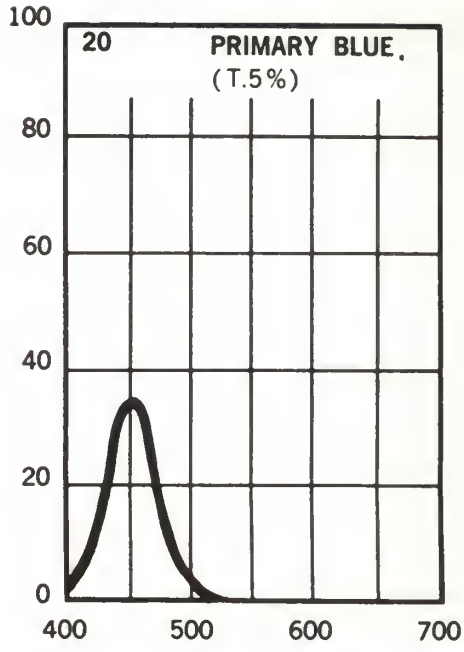
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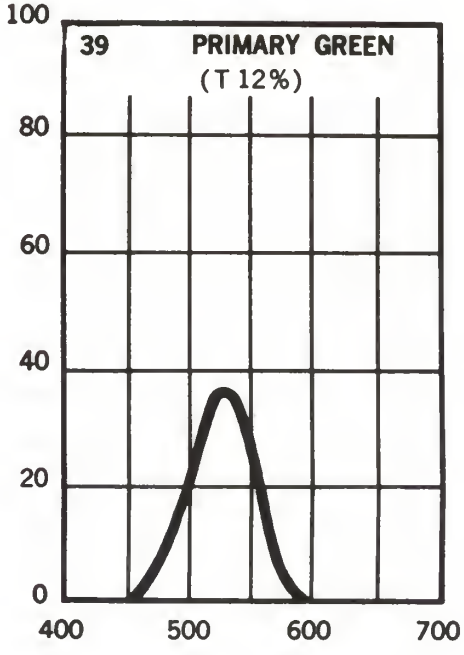
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PRIMARY GREEN
(T 12%)
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Table I. Germination of P. louisianica seeds under various light qualities at 24°C and 30°C.

Experimental conditions		Percent germination	
temperature	light quality	seedcoat removed	seedcoat intact
24°C	red	10-15	0
	green	10	0
	white	0	0
30°C	red	90-100	0
	green	85-95	0
	far red	0	0
	blue	0	0
	white	26	2

No comparable data were compiled using P. parviflora seeds. Red light at 30°C was used to germinate some embryos for seedling anatomy studies, resulting in 10-20% germination. These seedlings were placed in peat pots and kept in the 30°C growth chamber. Due to the great amount of evaporation that occurred within the chamber, all of the seedlings were lost by the end of one day. Therefore, it was necessary to germinate P. parviflora seeds with 50ppm GA_3 for the comparative anatomy studies.

Seedling anatomy

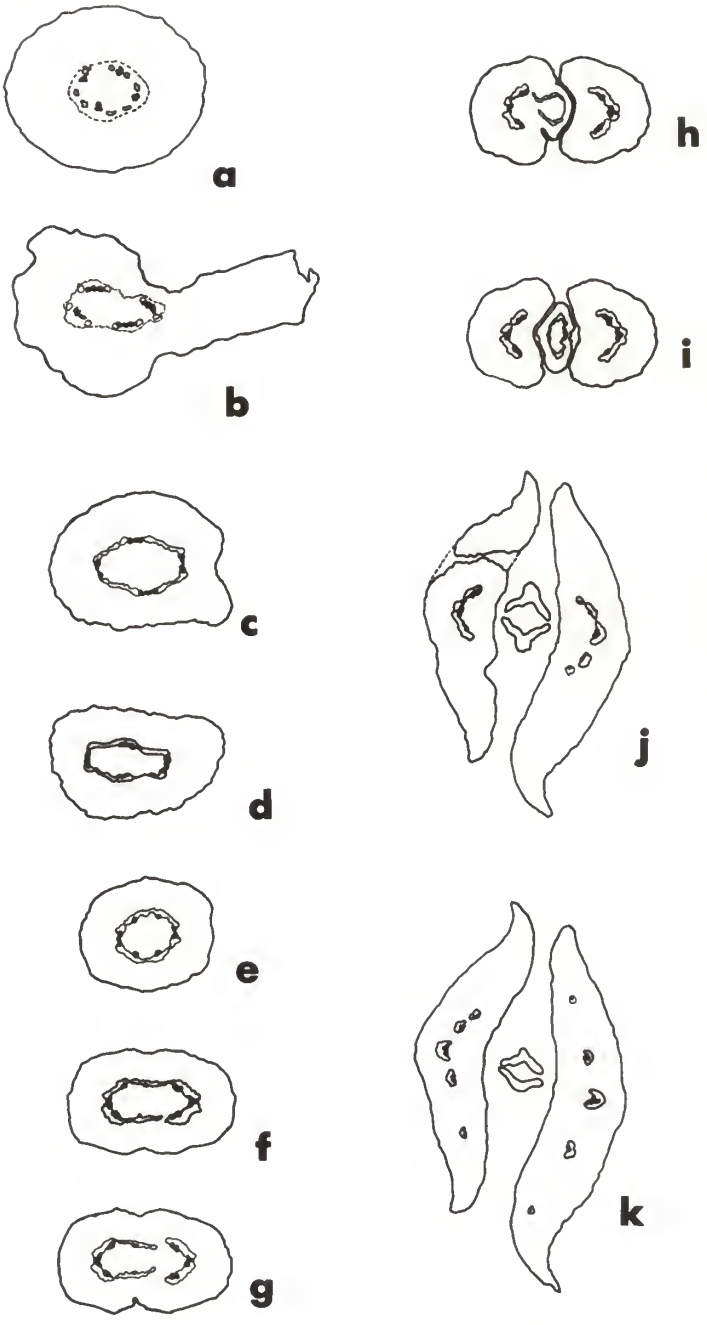
The exarch system of the radicle was tetrarch in P. parviflora and P. louisianica, and the features here described

were observed in both species. The endodermis was composed of tall, narrow cells with no noticeable Casparian strips, but it formed a starch sheath which continued into the epicotyl. Early during germination, a peg was formed at the base of the hypocotyl which held the seedcoat in place below the soil line and allowed the cotyledons to expand freely as the hypocotyl drew them into the atmosphere. This peg is parenchymatous, lacks any vascularization, and is oriented in the same plane as the cotyledons. The hypocotyl has a hypodermal layer of collenchyma 4-5 cells thick and a parenchymatous cortex. In the hypocotyl two bundles from the endarch maturation of as many poles of the stele maintained their integrity and became the midveins of the cotyledons. The remaining bundles split, half of each supplying the lateral veins of the cotyledons (Fig. 2). The cotyledons, which were auricled at their bases, had two layers of palisade parenchyma on their adaxial side; spongy parenchyma and three veins constituted the remainder of the cotyledonary tissue. Excised embryos which were used for this study carried the nucellus above ground until the expansion of the cotyledons ruptured it. The nucellus was 1-3 cells thick and was covered with a noncellular layer of material which stained only with safranin in all staining schedules used.

Nodal anatomy

The nodes of these two species were unilacunar with one trace. This condition was observed at three levels within

Fig. 2. Seedling vascularization of P. louisianica: a, root; b, hypocotyl peg; c-f, hypocotyl; g-i, cotylendonary node; j-k, cotyledons. Blackened areas represent xylem; associated white areas, phloem.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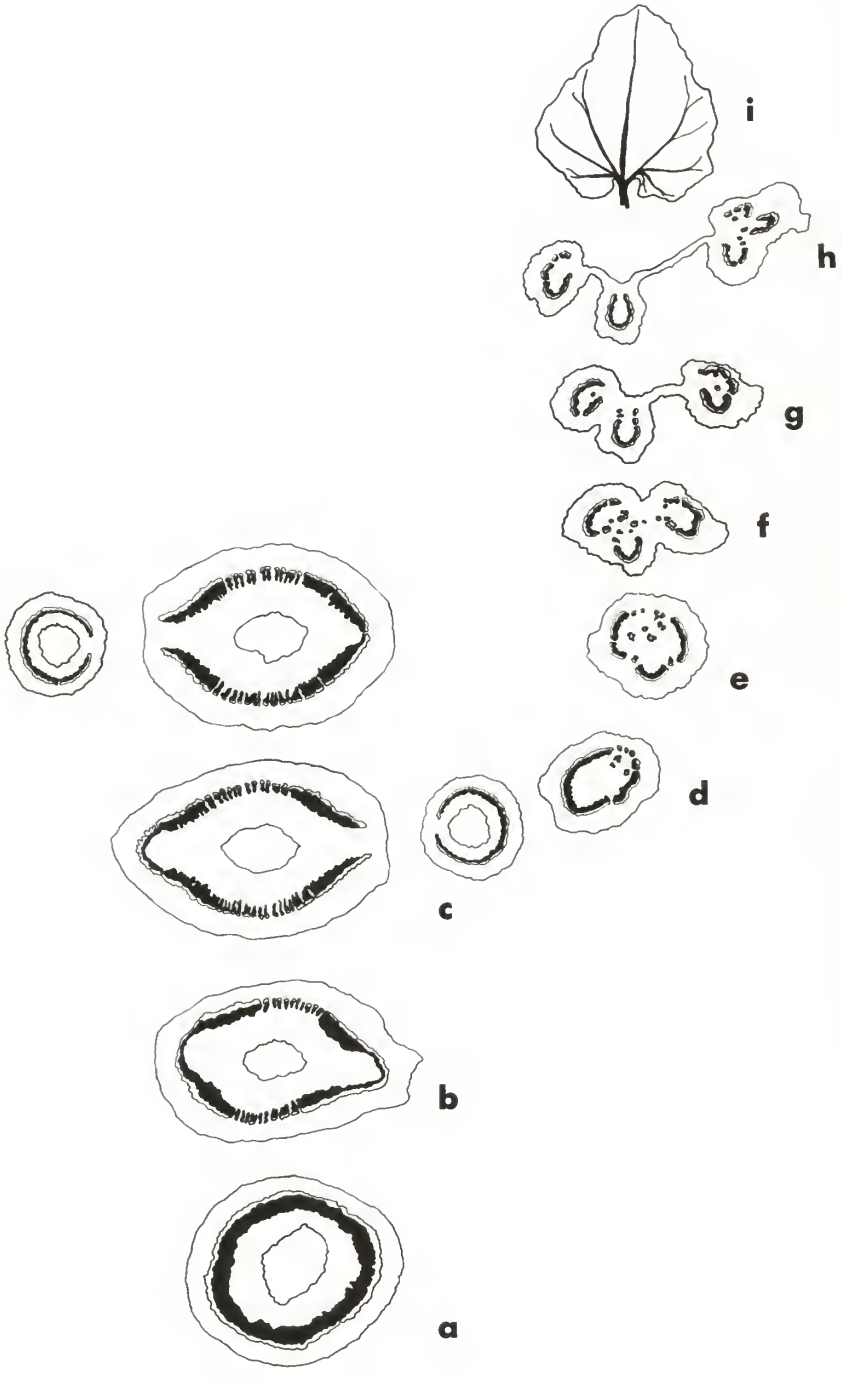
the plants and therefore was considered to be constant throughout the plants. The petioles had large lacunae within a centrally located cylinder of parenchyma. Degeneration of a portion of the parenchymatous core of the petiole was responsible for the formation of these lacunae. This condition was found in almost the entire length of the petiole; the proximal and distal ends did not have lacunae, therefore the chamber was not continuous with that of the stem (Fig. 3).

Stem anatomy

Epidermis. The epidermis of the stem was a single layer of cells, and in the older stem the outer tangential wall was considerably thicker than any of the other walls. The trichomes of the stem were glandular, being composed of a uniseriate, multicellular stalk and a multicellular head. The length of these trichomes ranged from 0.2 mm to 1.5 mm; the different lengths were found together. This type of trichome is discussed more fully under leaf anatomy.

Ground tissue. The cortex was composed of a continuous cylinder of lacunar collenchyma in the hypodermal area, and internal to this was a band of large, thin-walled parenchyma with many intercellular spaces. Starch grains and other inclusions were not noted in the collenchyma or parenchyma of the cortex with the exception of those cells which constituted a parenchymatous starch sheath (discussed under seedling anatomy). The cells which made up the starch sheath

Fig. 3. Camera lucida drawings of the unilacunar node of *P. louisianica* with its single trace: a-b, stem; c, stem with gap and base of petiole; d-f, petiole; g-h, base of lamina; i, schematic representation of the entire lamina illustrating its vascularization. Blackened areas represent xylem; associated white areas, phloem.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were much smaller radially than other cortical cells, but had the same tangential dimension. In young stems starch grains were present but were lacking in similar cells of older tissue.

Cells, that had the same radial and tangential dimensions as the starch sheath, were located between this sheath and the sieve-tube elements of the phloem and appeared parenchymatous in young stems but gave rise to clusters of fibers in older stems. These clusters of extraxylary fibers appeared somewhat equidistantly spaced in the stem, but the spacing was not in relationship to any given number of rays. In transections and macerations, fibers of two different sizes were found together: narrow, short ones and wide, long ones. The short fibers in P. parviflora were 1.47mm in length and 35.6 microns in diameter; the long fibers were 2.51 mm long and 56.6 microns wide. The short fibers in P. louisianica were 1.47 mm long and 30 microns wide; the long fibers, 2.2 mm long and 63.1 microns wide. The mean wall thickness was 6.0 microns for fibers of both sizes. These fibers had strongly tapered to rounded ends and simple pits.

The pith of both taxa contained thin-walled, large-celled parenchyma which degenerated early leaving a hollow cylinder.

Vascular tissue. Discrete groupings of sieve-tube elements occurred in the phloem. The sieve-tube elements had transverse end-walls with simple sieve plates limited

to the end-walls.

The stems of both populations studied have considerable secondary growth at the soil line, that is the stem at the first and possibly second nodes. For a comparison of selected features of the woods of P. parviflora and P. louisianica, see Table II.

Table II. Comparison of selected features of the woods of P. parviflora and P. louisianica.

Feature	P. parviflora	P. louisianica
number of vessels/mm^2	35.5[a]	34.6
number of vessels/group	3.2	2.8
vessel-element length		
root	192.0	178.3
stem	190.3	183.1
vessel-element diameter		
root	162.0	173.5
stem	127.2	138.8
angle of vessel-element end-wall [b]	10-25°	5-30°
length of libiform fibers	659	705
diameter of libiform fibers	20.6	26.2
ray width	97.0	88.3
ray height	0.34-1.1 mm	0.34-1.5 mm
number of rays/mm^2	10.0	6.6

a measurements are in microns unless otherwise noted

b angle from the horizontal

The vessel-elements had simple perforation plates and an alternate pitting pattern, with some of the pits being horizontally elongated. The end-walls vary in orientation from horizontal to somewhat oblique. The larger vessels were caudate, the more narrow vessels were not. Intravascular pitting on vessels was with bordered pits; vessel to fiber pitting was with half-bordered pits, vessel to ray parenchyma with half-bordered pits, and all other pit pairs were simple. The bulk of the xylem was made up of libiform fibers. The rays were all multiseriate and heterocellular. All ray parenchyma had secondary thickening of the walls.

Leaf anatomy

The stomates were anomocytic and oblong in face view. Mayberry (1947) stated that the number of stomates per square millimeter was "considerably below the commonly expressed average of 225 per sq. mm. of leaf surface." He found 30 stomates/sq. mm. on both surfaces of the leaf. It is my opinion that if reference to numbers of stomates is to be of any taxonomic value, these numbers should be expressed in relationship to unspecialized epidermal cells. According to Zalenski (Maximov, 1938, p. 369), epidermal cells of leaves decrease in size and increase in frequency from the basal to apical parts of a plant. This frequency increase of cells was also observed with regard to one organ, the number of cells increase with the distance from the main vascular supply. The frequency of stomates also increases acropetaly. Therefore, data given

as number of stomates per surface area should also include environmental conditions at the time of growth, point of attachment of the leaves measured, the size of the leaves, the portion(s) of the leaves from which the epidermis was removed, and if the leaf was a sun leaf or a shade leaf. Salisbury (1927) employed an expression, the stomatal index, to express the proportion of stomates to unspecialized epidermal cells. He defined the stomatal index as $I = \frac{S}{E + S} \times 100$. S was the number of stomates per unit area, and E the number of epidermal cells in the same unit area. He found this proportion to hold true for different parts of the same leaf, leaves from different parts of the plant studied, and leaves from plants of the same species grown in very diverse environs. Therefore, in this study, numbers of stomates for the taxa are expressed as stomatal indices (see Table III).

Table III. Stomatal indices of P. parviflora and P. louisianica.

species	surface	observed range of stomatal indices	mean of stomatal indices
	upper	25.0 - 27.1	26.1
P. parviflora			
	lower	25.9 - 29.0	27.9
	upper	21.7 - 25.9	24.1
P. louisianica			
	lower	26.1 - 30.0	28.1

The stomates of P. parviflora laminae ranged in size from 10-13 microns long and 7-9 microns wide; those of P. louisianica were 8-11 microns long and 6-8 microns wide.

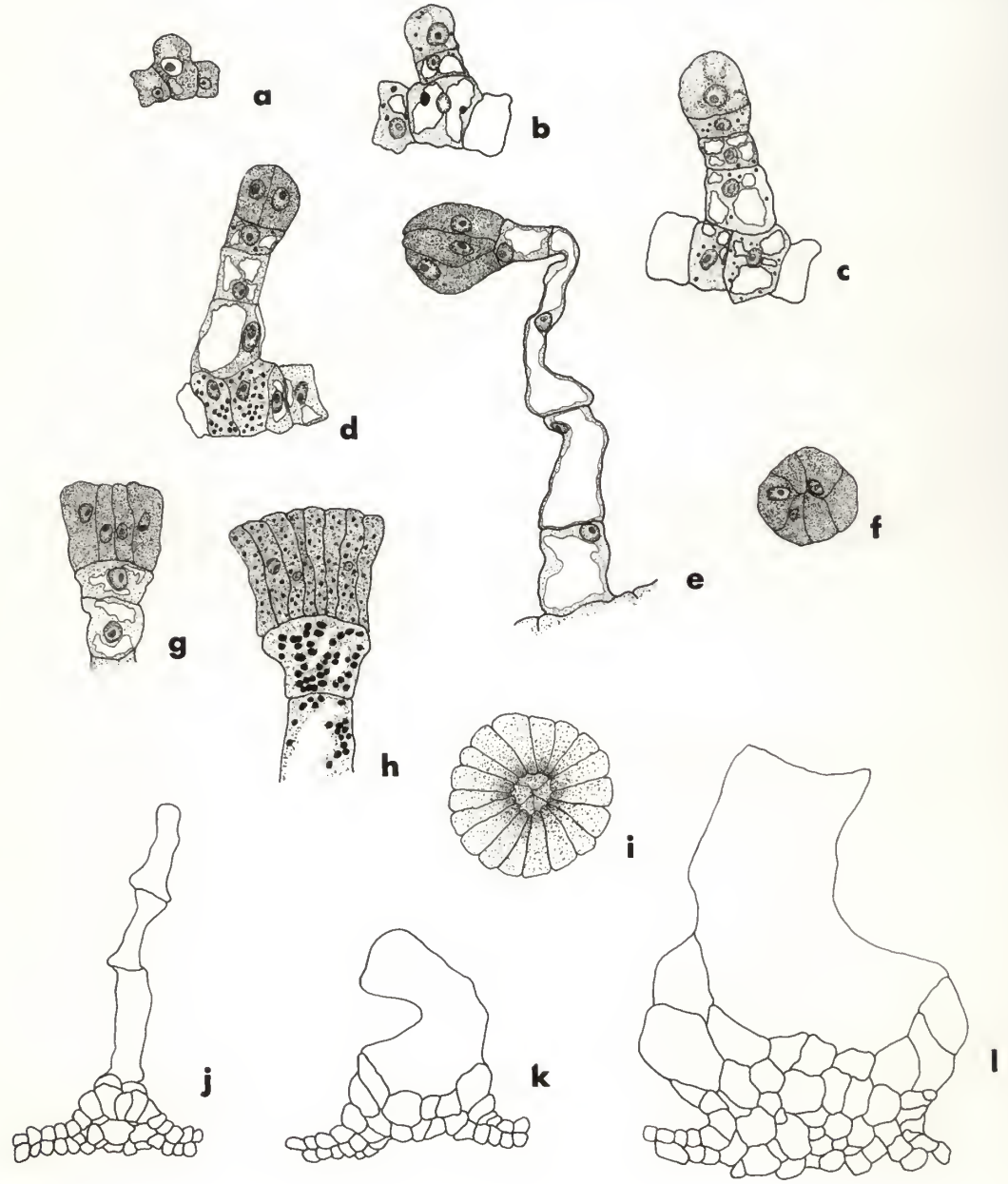
The trichome complement of the petiole and lamina of both taxa consisted of two types of glandular trichomes, but lacked the type of trichomes described as simple clothing hairs by Mayberry (1947). He did not discuss the makeup of this type of trichome, but his illustrations showed uniseriate trichomes 3 to 4 cells long with a pointed apical cell. My observations suggest that Mayberry's clothing hairs were possibly glandular trichomes from which the glandular head had been lost. Figure 8a and 8b show trichome complements of stem and leaf of P. louisianica respectively. Trichomes with glandular, multicellular (10-14 cells) heads and uniseriate stalks of 4-9 cells were found in great abundance on the petioles and laminae. This type of trichome developed from the outward growth of an epidermal cell and subsequent periclinal divisions to give rise to the uniseriate stalk. The basal cell undergoes anticlinal divisions resulting in the multicellular, raised base of this trichome type. The apical cell of this hair undergoes several divisions, laying down walls at right angles to the walls of the stalk cells (Fig. 4).

The second type of glandular trichome has been found only on the lamina. It consisted of a unicellular stalk and a 2-6 celled head. Solereder (1908) also described this

Fig. 8a. Trichome complement of the stem of P. louisianica; 33X.

Fig. 8b. The multicellular stalked, glandular trichomes of the leaf of P. louisianica; 32X.

Fig. 4. Trichome development on the stem of P. louisianica: a, original epidermal cell which gives rise to a trichome: b, trichome in the three-celled stage; c, trichome in the four-celled stage, the original epidermal cell has undergone an anticlinal division; d, the apical cell divides when the trichome is at the four-celled stage; e, glandular head beginning to develop by many divisions of the apical cell, the stalk cells becoming greatly vacuolated and elongated; f, top view of head when composed of six cells; g, side view of a six celled head; h, side view of mature head; i, top view of mature head; the center of the head is depressed; j-l, progressive stages in the development of the raised base of the trichome. Fig. 4a-4i, 370X; Fig. 4j-4l, 100X.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type of trichome on Martynia annua. This hair was derived from the outer cell of a cell pair; this pair resulted from a periclinal division of an epidermal cell (Fig. 5).

The single leaf trace divided to form a complete cylinder for the major portion of the petiole. At the distal end, the cylinder became dissected to supply the first marginal veins of the lamina. All of the bundles resulting from this dissection were collateral except a few small amphivasal bundles on the abaxial side of the petiole. This condition was noted in both species. The only mechanical tissue within the petiole, in addition to the vascular supply, is a hypodermal lacunar collenchyma layer of 4-6 cells.

The laminae of P. parviflora and P. louisianica were dorsiventral. The palisade parenchyma was two layers thick, the cells of the outer layer being two to three times as long as the cells of the second layer. The smaller veins of the leaves were located in the second layer of the palisade parenchyma. The larger vascular bundles had a narrow parenchyma sheath and collenchyma layers of two to three cells thick forming sheath extensions to each epidermis.

Floral anatomy

The vascular tissue of the pedicel was a cylinder similar to that of the stem and petioles, but there had been no breakdown of the central core of parenchyma. Single traces diverge from the cylinder to supply the subtending bracts.

Four pairs of bundles diverged from the stele to supply

the calyx. A total of 10 bundles left the stele to supply the corolla and andreocium. The bundles to the corolla and stamens were alternate in position. Each bundle supplying the corolla became dissected into three small bundles immediately upon entering the corolla. The last bundle of the andreocium to diverge from the stele supplied the rudiment of the fifth stamen (Fig. 6). The vascularization of the ovary consisted of two large, centrally located bundles which became reduced and disappeared by the top of the ovary, numerous small bundles of the ovary wall, and two intermediate sized bundles which were located in the ventral and dorsal peripheries of the ovary. These latter bundles supplied the style (Fig. 7).

The calyx tissue was composed of thin-walled parenchyma with large intercellular spaces. The vascular bundles were included within parenchymatous sheathes which extended from the inner to the outer epidermis. Glandular trichomes, the type having 10-14 cells in the head, were found on each epidermis, but with a higher number being on the outer. The tissue of the corolla was of thin-walled parenchyma and was 5-7 cells thick.

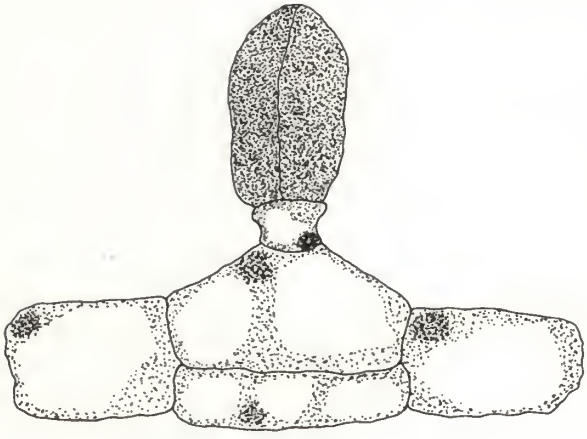
Fruit anatomy

The fruit of P. parviflora was anatomically similar to that described for P. louisianica (Mayberry 1947). The pericarp differentiated into exocarp, mesocarp, and endocarp.

Fig. 5. Camera lucida drawing of the unicellular stalked trichome of P. louisianica leaf. Approximate magnification, 1350X.

Fig. 6. Floral vascularization of P. louisianica and P. parviflora. The outer whorl, calyx; middle whorl, corolla; inner whorl is the vascularization of the androecium with cross-hatching that of the staminode.

Fig. 7. Pistil vascularization of P. louisianica and P. parviflora.



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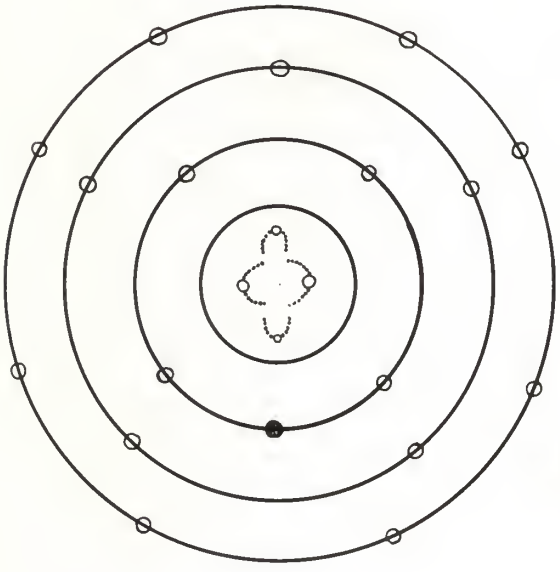

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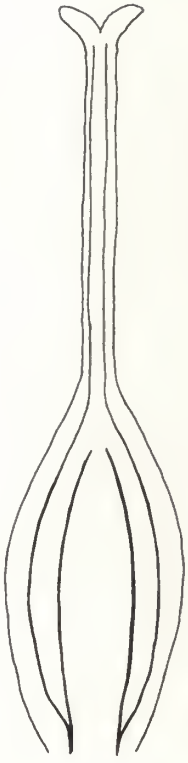

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The exocarp was the epidermis, and the mesocarp was of thin-walled parenchyma containing scattered vascular bundles; those cells of the mesocarp which were in close proximity with the exocarp were smaller in size than those in the remainder of the mesocarp. The endocarp was composed of interwoven strands of sclerenchymatous fibers, which were lignified in the mature fruit. The sclerenchyma of the endocarp extended into the apex of the mature fruit and thus when the exocarp and mesocarp were sloughed off, the stony extensions of the sclerenchyma formed the horns so characteristic of these fruits.

DISCUSSION

The light-sensitivity of seeds of several species of plants has been observed. Toole et al.(1956) listed the seeds of five species which were sensitive to light; in particular, germination was stimulated by red light and inhibited by far-red light. Intact seeds of P. louisianica did not germinate under any light; Anderson (in press) suggests that there is a water soluble inhibitor in the seedcoat. Excised embryos, exhibited a significant stimulation of germination under red light. There was also observed a stimulation of germination under the green light system used. The light systems used in this study, the filter and the initial light source, may not have provided red light and green light as "clean" as had been desired. The filter used for the transmittance of green light allowed the transmittance of some light at 6000A to about 6500A, therefore it cannot be concluded that the

stimulation to germination was due wholely to the green light. Apparently there was a temperature-light quality interaction involved in the germination, as was observed in the differences between germination percentages of seeds at 24°C and 30°C. Day length was not a factor in the percentage differences in this study because the seeds were maintained at 16 hours of light a day.

The anatomy of the P. parviflora and the P. louisianica populations studied was very similar. Both taxa had tetrarch xylem in the radicle of the seedlings, and in the hypocotyl two of the poles of the initial tetrarch arrangement retained their integrity to become midveins of the cotyledons. The trichome complements of these two species were composed of one type of glandular trichome on the stem and petiole, and of two types of glandular trichomes on the leaves. No clothing hairs were observed as mentioned by Mayberry (1947). The stems of the two species had a single-celled layer of the inner portion of the cortex in which starch grains were numerous. This layer of cells was a starch sheath which Esau (1965) considered to fit the definition of an endodermis. Mayberry, in his anatomical study of P. louisianica (1947), showed this sheath in his illustrations but made no reference to it in the text. The range in vessel-element lengths and diameters was about the same for both taxa. A statistical analysis of the variations encountered in vessel-element lengths and diameters supports the contention that the vessel-elements came from only one population.

All of the anatomical characteristics considered in this study were similar for the two populations observed. These findings suggest that the species P. parviflora and P. louisianica are very closely related species or possibly infraspecific variations of the same species. However, they may represent sibling species. Therefore, to determine which of these possibilities is actually true, a detailed breeding program would be necessary.

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ANATOMIC STUDIES ON PROBOSCIDEA PARVIFLORA AND PROBOSCIDEA LOUISIANICA

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A descriptive anatomic study of Proboscidea parviflora and P. louisianica, to include effects of different light qualities upon seed germination, is reported. Germination of excised embryos of P. louisianica is stimulated by the red light and the green light systems used. Observations suggest a temperature-light quality interaction. Anatomic features such as tetrarch xylem of the root, a starch sheath and extraxylary fibers of the stem, unilacunar nodes with a single trace, floral vascularization, and the trichome complements (to include the ontogeny of glandular trichomes) are reported. Comparison of observed characteristics shows no anatomical distinction between the species studied.